

Howling by coyotes (*Canis latrans*): variation among social classes, seasons, and pack sizes

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Abstract: From January 1991 to June 1993 we observed 54 coyotes (*Canis latrans*) for 2507 h in Yellowstone National Park, Wyoming, during which we observed 517 howling events. Among coyotes of different types of social organization (resident versus transient), members of resident packs initiated or participated in howling events, while transient individuals were never observed howling ($n = 51$ h of observation). For members of resident packs, alpha coyotes spent more time howling and had a higher rate of howling events than beta coyotes and pups; beta coyotes and pups howled similarly. The percentage of time and the rate of howling events typically peaked in the dispersal and breeding seasons, with the lowest rate of howling during pup rearing. Social rank and season did not influence the length of howling events. Pack size did not affect howling rates among individuals in a pack or the alpha pair. With respect to space-use patterns, coyotes in resident packs howled more frequently than expected along the periphery of the territory than in the core area. We concluded that, like wolves (*Canis lupus*), all coyotes in the resident pack did not contribute equally to howling duties; alpha coyotes howled more than all coyotes. Howling by coyotes appears to serve a territorial spacing function that is mainly performed by the alpha pair of the resident pack.

Résumé : De janvier 1991 à juin 1993, nous avons observé 54 Coyotes (*Canis latrans*) du parc national de Yellowstone, Wyoming, pendant 2507 h au cours desquelles nous avons enregistré 517 scéances de hurlements. Chez les coyotes à organisation sociale variable (individus résidents vs individus de passage), nous avons observé que les meutes de résidents étaient les instigateurs des scéances de hurlements ou y participaient, alors que les individus de passage n'ont jamais été surpris à hurler ($n = 51$ h d'observation). Chez les membres des meutes de résidents, les coyotes alpha passaient plus de temps à hurler et participaient à un taux plus élevé de scéances de hurlements que les coyotes bêta ou les juvéniles, lesquels avaient des hurlements semblables. Le pourcentage de temps passé à hurler et la fréquence des scéances de hurlements étaient maximaux au cours des saisons de dispersion et de reproduction et les taux les plus faibles ont été enregistrés au cours de la saison d'élevage des jeunes. Le rang social et la saison n'avaient pas d'influence sur la durée des scéances de hurlements. La taille de la meute n'affectait pas la fréquence des hurlements chez les individus de la meute ou chez le couple alpha. D'un point de vue spatial, les coyotes des meutes de résidents hurlaient plus fréquemment que prévu à la périphérie du territoire comparativement aux coyotes du coeur du territoire. Il faut conclure qu'à l'instar des Loups gris (*Canis lupus*) les coyotes de la meute de résidents ne contribuent pas tous également aux hurlements; les coyotes alpha sont ceux qui hurlent le plus. Les coyotes alpha augmentent la fréquence de leurs hurlements en hiver, sans doute à cause de l'augmentation des taux d'agression, de la défense territoriale plus intense et des changements hormonaux reliés à la saison de reproduction. Chez le Coyote, les hurlements semblent également servir à l'espacement territorial, une fonction assurée surtout par le couple alpha de la meute des résidents. [Traduit par la Rédaction]

Introduction

Communication by means of howling or vocalization is very common among members of the family Canidae (Mech 1970; Gier 1975; Harrington and Mech 1978b; Lehner 1978). Studies of wild canids in North America have identified many different types of vocalization (Theberge and Falls 1967; McCarley 1975; Harrington and Mech 1978b). Most of the field research on wild canid vocalizations has focused on wolves (*Canis lupus*), using rates of response to simulated

howling (Harrington and Mech 1982; Fuller and Sampson 1988). Studies indicate that wolf howling is used to reunite separated pack members, wolf packs respond more frequently near kills, alpha males are more responsive than other pack members, and howling serves as a territory-independent spacing mechanism (Harrington and Mech 1978a, 1978b, 1979, 1983). Previous research on coyotes (*Canis latrans*) has documented the types of vocalization (McCarley 1975; Lehner 1978), seasonal and diel variation (Laundre 1981; Walsh and Inglis 1989), and the influence of lunar phase (Bender et al. 1996), but little else is known about factors influencing coyote vocalization rates, particularly in reference to differences among types of social organization and among members of different social ranks within a resident pack of coyotes.

Coyotes communicate using auditory, visual, and olfactory cues (Lehner 1978). The coyotes in Yellowstone National Park provided a unique opportunity to increase our understanding of coyote communication because of the ease of identifying and observing individual free-ranging coyotes. During the collection of behavioral observations on coyote

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foraging ecology and predation (Gese et al. 1996b, 1996c), we found that in the case of olfactory communication (i.e., scent marking), alpha coyotes performed most of the scent-marking duties, rates of scent marking varied seasonally, pack size did not influence scent-marking rates, and scent marks were located more than expected along the periphery of the territory (Gese and Ruff 1997). Thus, of interest was whether a study of vocal communication (howling) would show similar results to olfactory communication (scent marking). Therefore, the specific questions we address in this paper are (i) Does howling vary with social organization (resident versus transient)? (ii) Does howling vary with social class (dominance rank) within a resident pack? (iii) Do rates of howling vary among seasons? (iv) Does pack size influence the rate of howling events (i.e., is howling a duty shared equally among pack members)? (v) Do coyotes howl with equal frequency throughout their territory? (vi) Do coyotes that later disperse contribute less to the howling rates of the pack compared with philopatric individuals?

Methods

Observations of howling by coyotes were recorded during collection of data on coyote foraging ecology and predation (Gese et al. 1996b, 1996c) in the Lamar River valley, Yellowstone National Park, Wyoming (44°52'N, 110°11'E). Elevation of the study area was about 2000 m. Winters are long and cold, with most of the annual precipitation falling as snow (Dirks and Martner 1982; Houston 1982). Habitats identified in the study area included forest, grassland, sagebrush-grassland, riparian areas, mesic meadow, and mesic shrub-meadow (for a description see Gese et al. 1996b).

Coyotes were captured with padded leg-hold traps with attached tranquilizer tabs (Balser 1965). Each coyote was immobilized (Cornely 1979) for handling and processing, then sexed, ear-tagged, and radio-collared. We extracted the first vestigial premolar from the lower jaw to estimate age by analysis of cementum annuli (Linhardt and Knowlton 1967). Pups were captured at the den when 10–12 weeks old and surgically implanted with an intraperitoneal transmitter. Individuals were classified as pups (<12 months old), yearlings (12–24 months old), or adults (>24 months old). Coyotes were also classified as members of a resident pack or as transient individuals (Bowen 1978; Gese et al. 1988). Residents were classified into three different social classes: alpha coyotes (the dominant, breeding adult male and female), beta coyotes (adults and yearlings subordinate to alpha coyotes but dominant over pups), and pups (young of the year, subordinate to both alpha and beta coyotes) (Schenkel 1947, 1967; Rabb et al. 1967; Mech 1970). Coyotes were reclassified into the next age or social class as they grew older.

Behavioral observations of radio-collared, implanted, and unmarked coyotes were made using a 15–30× spotting scope from a vehicle or from observation points on hills overlooking the valley, and followed the sampling procedures described in Gese et al. (1996b, 1996c). We used focal-animal sampling (Lehner 1979), recording behaviors continuously on a computer, or on a tape recorder for later transcription. All howling events were documented during behavioral observations. A series of howls by an individual coyote was counted as a single howling event. A howling event by an individual may stimulate other pack members to join in a group howl, but we recorded the time and length (in seconds) of the howl by the individual coyote we were observing only. One minute of silence signalled the end of the howling event (Harrington and Mech 1978a). We standardized the rate of howling as the number of events observed per hour. The senior author trained all observers for 5–7 days to maintain consistent interpretation and recording of behaviors (Lehner 1979; Martin and Bateson 1993). Most observations were

made during daylight hours (07:00–20:00) from October to July; high grass in August and September prevented data collection. Nocturnal observations were also conducted with a night-vision scope (Litton Electron Devices, Tempe, Arizona). Whenever possible we recorded the location of howling events to the nearest 10 m grid intersection on a 1 : 24 000 U.S. Geological Survey topographic map, using the Universal Transverse Mercator grid system. Based upon dates of observed courtship behavior, copulations, and pup whelping, we divided the period of data collection into 4 biological seasons: breeding (16 December – 15 February), gestation (16 February – 15 April), pup rearing (16 April – 15 July), and dispersal (15 October – 15 December).

We examined the influence of social rank, season, year, and pack on percent time spent howling, howling rate, and length of a howling event, using multiway analysis of variance (ANOVA) in a factorial design (Steel and Torrie 1980; Sokal and Rohlf 1981). The sampling unit for the ANOVAs was the individual coyote per season (Machlis et al. 1985; Morrison et al. 1992). Pairwise comparisons were performed using Tukey's multiple comparisons test where one-way ANOVAs indicated a significant difference between groups. The relationship between pack size and percent time spent howling and howling rate was examined with regression analysis. The frequency of howling events in relation to space use was examined with χ^2 tests. All statistical tests were performed using SYSTAT (Wilkinson et al. 1992).

Results

We observed a total of 54 coyotes from January 1991 to June 1993, during which period we noted 517 howling events. Of the 54 coyotes, 49 were members of resident packs and 5 were transient individuals. The five resident packs and transients were observed for 2456 and 51 h, respectively. Thirty-one coyotes were equipped with radio collars or carried implanted transmitters, and 23 animals were not marked but were recognized from physical characteristics. We observed 29 males and 23 females; 2 unmarked coyotes were of unknown sex. For more details on the individuals observed and pack histories see Gese et al. (1996a, 1996b).

Influence of social organization and social rank

The first level of analysis examined the influence of social organization (resident versus transient) on howling rates. Among members of a resident pack, the mean howling rate for alpha and beta coyotes and pups was 0.33, 0.10, and 0.11 events/h observed, respectively. In contrast, during the collection of 51 h of observation on five transient coyotes, not a single howling event was documented. Thus, only members of the resident pack were observed to initiate or participate in howling.

The second level of analysis examined the influence of social rank within the resident pack on howling by coyotes. We found that the social rank of a coyote and the season were significant factors influencing percent time spent howling (Table 1). For all seasons combined, alpha coyotes spent more time howling (\bar{x} = 0.59%) than beta coyotes (\bar{x} = 0.15%) and pups (\bar{x} = 0.14%) (P < 0.001); beta coyotes and pups spent similar percentages of time howling (P = 0.998). During the breeding, gestation, and dispersal seasons, alpha coyotes spent more time howling than beta coyotes and pups (P < 0.05) (Fig. 1); however, percent time spent howling did not differ significantly among the social ranks during the pup-rearing season (P > 0.15) (Fig. 1). Alpha coyotes spent more

Table 1. Influence of sex, social rank, season, year, and pack on the percentage of time spent howling, rate of howling, and length of the howling event for coyotes in the Lamar River valley, Yellowstone National Park, Wyoming, from January 1991 to June 1993.

Source	df	ANOVA					
		Time spent howling (%)		Rate of howling		Length of howl	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Sex ^a	1	0.322	0.571	0.001	0.990	0.964	0.328
Social rank ^b	2	17.024	<0.001	25.701	<0.001	1.744	0.179
Season ^c	3	4.001	0.008	8.423	<0.001	1.891	0.135
Year ^d	2	0.501	0.607	1.323	0.268	1.285	0.280
Pack ^e	4	0.966	0.427	0.243	0.914	3.157	0.017
Error	225						

^aMale or female.

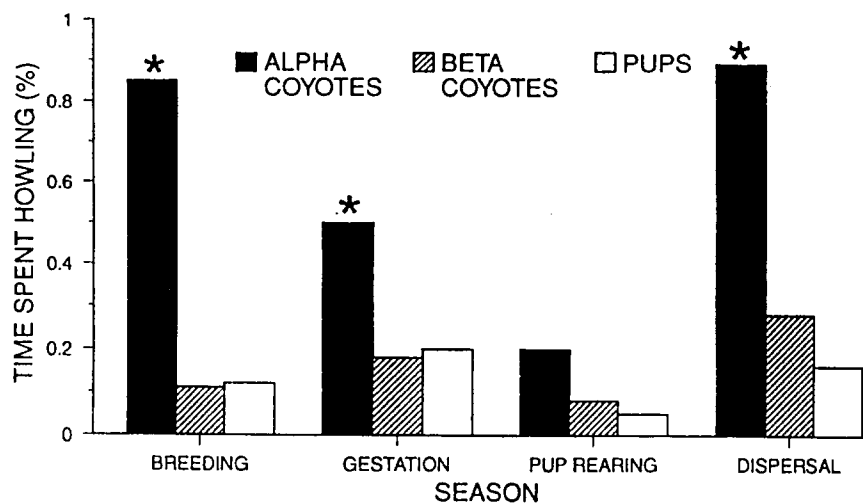
^bAlpha, beta, or pup coyote.

^cBreeding, gestation, pup rearing, or dispersal.

^d1991, 1992, or 1993.

^eBison, Druid, Fossil Forest, Norris, or Soda Butte.

Fig. 1. Mean percentages of time spent howling by alpha and beta coyotes and pups during 4 biological seasons in Yellowstone National Park, Wyoming, from January 1991 to June 1993. An asterisk denotes a significant difference among social ranks in that season ($P < 0.05$).



time howling during the breeding, gestation, and dispersal seasons than during the pup-rearing season ($P < 0.04$). The amount of time beta coyotes and pups spent howling did not differ among all seasons (beta coyotes: $P > 0.20$; pups: $P > 0.60$).

We found that the rate of howling (number of events/h) was similarly influenced by social rank and season (Table 1). Alpha coyotes howled at a higher rate than beta coyotes and pups during the breeding, gestation, and dispersal seasons ($P < 0.05$). There were no differences in howling rate among social ranks during the pup-rearing season (Fig. 2). Alpha coyotes howled at a lower rate during pup rearing than in all other seasons ($P < 0.02$); beta coyotes and pups showed no differences in howling rate during all seasons (Fig. 2).

We found that though the mean length of a howling event was not influenced by any social factor, there were differ-

ences in two of the five resident packs (Table 1). The only significant difference was that, on average, howling events were shorter ($P = 0.030$) for the Fossil Forest pack ($\bar{x} = 47$ s) than for the Soda Butte pack ($\bar{x} = 72$ s); the lengths of howling events did not differ significantly for all other packs ($P > 0.10$). The reason for the difference between these two packs is unknown. The average lengths of howling events did not differ among all social ranks and seasons (Fig. 3).

Locations of howling events

Scent marking among coyotes occurs more frequently along the periphery of the territory than in the core area (Wells and Bekoff 1981; Gese and Ruff 1997). Thus, we were also interested in examining whether coyotes howl more frequently along the edge of their territory than in the core area. We used the Fossil Forest pack to examine the spatial relations of

Fig. 2. Mean howling rates for alpha and beta coyotes and pups during 4 biological seasons in Yellowstone National Park, Wyoming, from January 1991 to June 1993. An asterisk denotes a significant difference among social ranks in that season ($P < 0.05$).

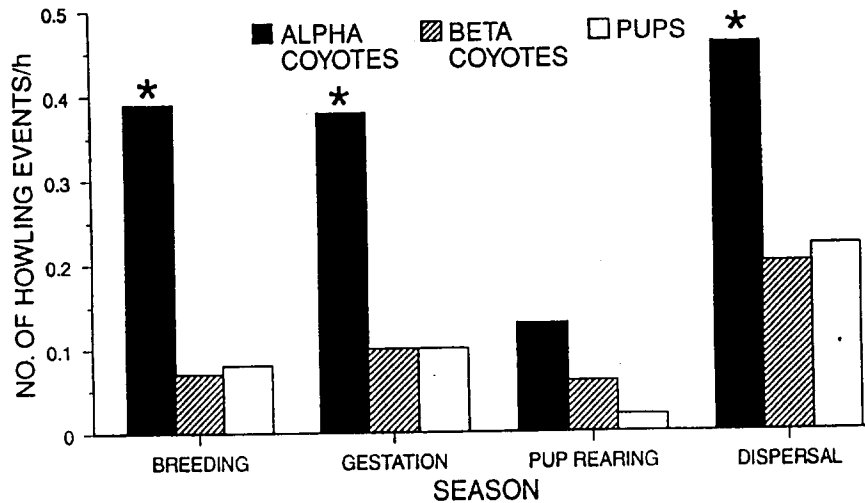
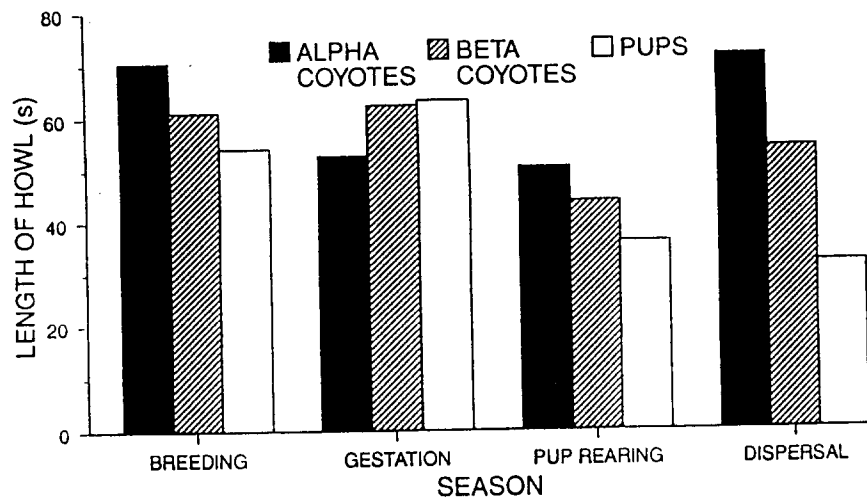


Fig. 3. Mean lengths of howling events for alpha and beta coyotes and pups during 4 biological seasons in Yellowstone National Park, Wyoming, from January 1991 to June 1993.



howling because we were able to observe the pack members throughout their territory and we maintained visual contact for 97% of the time during 593 h of observation. Locations of howling events were classed as being either in the core area or along the edge of the territory (i.e., <250 m from the territorial boundary; Bowen and Cowan 1980; Gese and Ruff 1997). The boundary was determined by visual observations of scent marking and territorial defense. The territory is bounded by a high, steep escarpment along the western border (Fig. 4A) that was not used or occupied by an adjacent coyote pack; thus, this area was not classified as periphery (Gese and Ruff 1997).

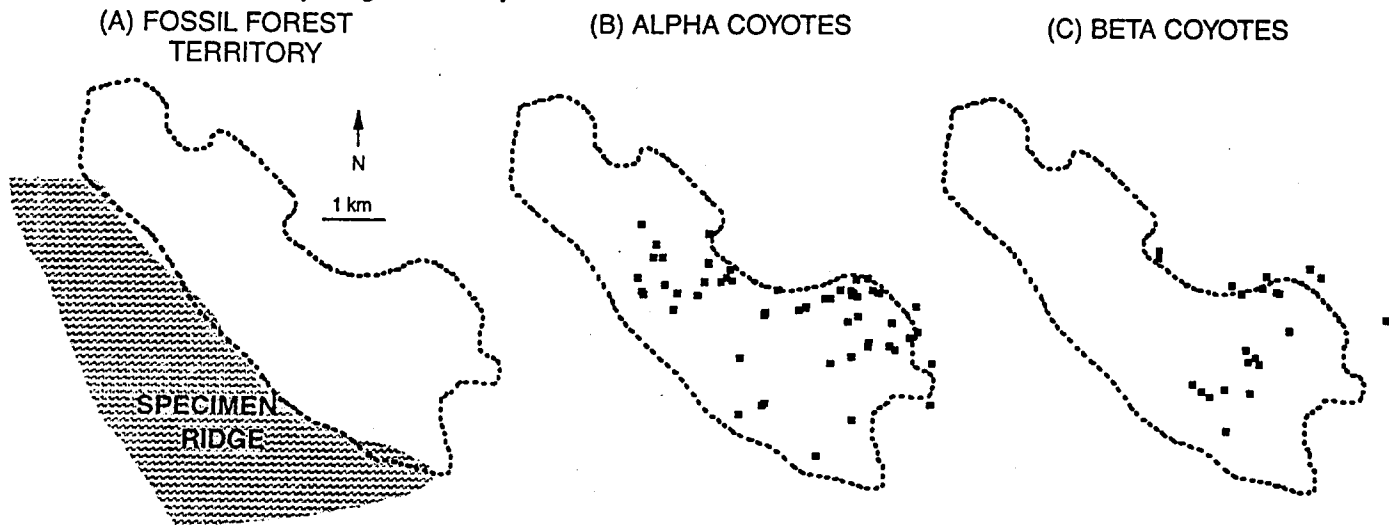
The Fossil Forest pack spent 33% of its time along the periphery of the territory. Thus, using 33% as the expected value for the amount of time spent along the periphery, we found that the alpha coyotes performed 56% of their howling events along the territorial border ($\chi^2 = 18.40$, 1 df, $P = 0.0001$) (Fig. 4B). Similarly, the beta coyotes performed 56% of their howling events along the border ($\chi^2 = 5.98$, 1 df, $P =$

0.014) (Fig. 4C). The periphery of the Fossil Forest territory constituted 26% of the area. Thus, if 26% is used as the expected value for the amount of area along the periphery, both the alpha and the beta coyotes performed more howling events than expected along the periphery and fewer than expected in the core area (alpha coyotes: $\chi^2 = 36.21$, 1 df, $P = 0.0001$; beta coyotes: $\chi^2 = 11.69$, 1 df, $P = 0.0006$).

Howling among dispersing versus philopatric coyotes

Certain members of each resident coyote pack dispersed throughout the year (Gese et al. 1996a). These dispersing individuals typically had less access to ungulate carcasses and were less successful hunters of small mammals during times of increased pack size compared with philopatric coyotes (Gese et al. 1996a). We were interested in examining the following question: If a coyote is not allowed equal access to food and will soon disperse from the territory, will this future disperser contribute less in terms of howling than siblings that remain (i.e., philopatric coyotes)? All comparisons involved animals

Fig. 4. Location of the Fossil Forest pack territory (A) and howling locations of alpha (B) and beta coyotes (C) of the Fossil Forest pack, Yellowstone National Park, Wyoming, from January 1991 to June 1993.



described in Gese et al. (1996a). Values for dispersing coyotes are from the period 2–3 months prior to their dispersal. We found that both philopatric coyotes ($n = 31$) and coyotes that later dispersed ($n = 7$) had an average howling rate of 0.18 events/h observed ($t = -0.056$, 36 df, $P = 0.956$). Philopatric coyotes and animals that later dispersed spent an average of 0.22 and 0.09% of their time howling, respectively ($t = 0.785$, 36 df, $P = 0.437$). We concluded that coyotes that later dispersed howled similarly to animals that were philopatric.

Influence of pack size

The formation of large packs of coyotes and wolves may be beneficial in that the duties of food acquisition and defense, care of offspring, and territorial defense are shared (Mech 1970; Camenzind 1978; Bekoff and Wells 1986). We demonstrated that the alpha coyotes in the resident pack spend more time howling, and howl at a higher rate, than the beta coyotes and pups (Figs. 1 and 2). However, we were also interested in examining whether pack size affected the rates of howling by all members in the pack, as well as of the alpha pair (i.e., whether individual coyotes in larger packs howl less frequently than animals in smaller packs). Using regression analysis, we examined the relationship between pack size and each individual's rate of howling for each season over the 3 years of study. We found no significant relationship between pack size and rate of howling by each individual in the pack ($R^2 = 0.008$, $F_{[1,160]} = 1.238$, $P = 0.27$). Similarly, we examined the following question: Does pack size influence the rate of howling by the alpha pair (i.e., do alpha pairs in large packs howl less frequently than alpha pairs in small packs)? We found that the rate of howling by the alpha pair was independent of pack size ($R^2 = 0.001$, $F_{[1,95]} = 0.055$, $P = 0.81$). We concluded that pack size did not influence the rate of howling by individuals in the pack or by the alpha pair. The alpha pair performs most of the howling in the resident pack.

Discussion

Howling is an important means of communication among large carnivores (Mech 1970; Lehner 1978). Among wolves,

much is known about the types of howls produced, the frequency and location of howling, and the role possibly played by howling in territorial maintenance (Theberge and Falls 1967; Harrington and Mech 1978b, 1979, 1983). In the case of coyotes, the only studies on free-ranging animals have examined the types of howls produced and the seasonal and diel patterns of howling (McCarley 1975; Lehner 1978; Laundre 1981; Walsh and Inglis 1989). However, little is known about the role of social rank in determining coyote howling rates because previous studies usually did not identify the coyotes producing the howls. Our observations in Yellowstone National Park provided data on rates of howling by coyotes whose identity was known.

We found that transient coyotes did not howl during 51 h of observation. Harrington and Mech (1979) reported that single lone wolves never replied to simulated howling; lone wolves only replied when with other lone wolves at a kill. We also found that transient coyotes scent-marked at rates far below those of resident coyotes (Gese and Ruff 1997), as was found in wolves (Rothman and Mech 1979). Scent marking and howling serve a role in territorial maintenance. Thus, since transient coyotes, like lone wolves, do not have a territory to defend, there is little need to advertise their presence. Harrington and Mech (1979) reported that lone wolves appear to maintain a "low profile," attracting little attention and avoiding territorial wolves. Our observations on coyote scent marking (Gese and Ruff 1997) and howling support the "low profile" hypothesis for transient coyotes.

We found that social rank of the coyote and season influenced both the percentage of time spent howling and the rate of howling. The alpha coyotes spent more time howling and howled at a higher rate than the beta coyotes and pups. Among the alpha coyotes, howling peaked in winter during the dispersal and breeding seasons and rates were lowest during the pup-rearing season. Subordinate coyotes (beta coyotes and pups) showed no seasonal change in howling rates. Harrington and Mech (1979) found a similar peak in howling rates during the winter for wolves in northeastern Minnesota and correlated this increase with the breeding season. Klinghammer and Laidlaw (1979) reported that spontaneous

howls in a captive wolf pack peaked during the breeding season. Laundre (1981) documented 51 coyote vocalization bouts and reported an increase in the rate of vocalization in February–March, August, and November. In southern Texas, Walsh and Inglis (1989) found that the highest rates of coyote vocalization bouts occurred during February. Seasonal changes in howling rates among alpha animals may be related to increased pair-bond behavior and territorial maintenance during the breeding season, with the decline possibly related to a reduced need to advertise their presence outside of the breeding season. Increased howling rates during the breeding season may be correlated with the increase in aggression towards intruders (Zimen 1976; Harrington and Mech 1978b) and related hormonal changes (Klinghammer and Laidlaw 1979). Among Yellowstone coyotes, extraterritorial movements and dispersal typically occurred during fall and winter (Gese et al. 1996a), therefore less howling during summer may be related to a reduction in the need to defend the territory against potential intruders. Vulnerability of pups to other predators may also play a role in the reduced rates of vocalization by the alpha pair during the pup-rearing season (Joslin 1967; Harrington and Mech 1978b). However, coyotes still howled at or near den sites in Yellowstone National Park (Hatier 1995). Breeding female hyenas (*Crocuta crocuta*) whooped at the communal den to deter potentially infanticidal non-clan hyenas from approaching the cubs (East and Hofer 1991b).

We found that the alpha coyotes howled more frequently than the beta coyotes and pups. Harrington and Mech (1979) documented that alpha wolves replied to simulated howls more frequently than subordinate pack members did. High-ranking female hyenas vocalized at a higher rate than subordinates as a means of exerting dominance when gaining access to kills (East and Hofer 1991b). Harrington (1987) reported that aggressive howling by wolves is likely a signal of body size. An honest signal (Krebs and Davies 1987) of body size by the animal producing the signal would be important should an encounter lead to an aggressive confrontation with an intruder or a subordinate. The alpha pair, particularly the alpha male, was involved in most territorial defense involving direct confrontation with an intruder (E.M. Gese, unpublished data). The alpha male was typically the largest member of the coyote pack in our study area.

Coyotes and wolves display a repertoire of vocalizations (Theberge and Falls 1967; McCarley 1975; Harrington and Mech 1978b). Tooze et al. (1990) documented that among seven captive wolves, individuals displayed distinct vocalization patterns. East and Hofer (1991a) found that among spotted hyenas, the composition of whooping bouts varied among cubs, adult males, and adult females. We found that the length of a howling event was not influenced by the social rank of the coyote or by the season. Apparently, the type or composition (frequency, pitch) of the howl is more important in communicating information to other animals than the length of the howl.

The location of a howling event has received scant attention in canid research. For far-ranging canids, such as the wolf, there remains the difficulty of documenting spontaneous howls over a large area or territory. The only study involving spontaneous howling by wolves focused on dens and rendezvous sites (Harrington and Mech 1978a). Simu-

lated howls have been used to elicit responses from wolves in various parts of their territory (Harrington and Mech 1983), but the rate of spontaneous howls remains unknown. We were able to document the locations of spontaneous howls performed by coyotes throughout a pack's territory. Considering the amount of time spent along the periphery, and the area of the territory that was classed as periphery, we found that resident coyotes howled more frequently than expected along the periphery of the territory than in the core area, as with scent marking (Gese and Ruff 1997). While howling is a means of long-distance communication (McCarley 1975), resident coyotes would maximize the range of vocalization by howling more frequently along the edge of a territory. These vocalizations would then reach all adjacent packs and potential intruders. Thus, we conclude that howling acts as an advertisement of territorial possession, and plays a role in territorial maintenance and pack spacing.

Harrington and Mech (1978b) reported that pack size influenced the response rate of wolves to simulated howling. We tested the hypothesis that if all pack members contribute equally to howling, then individuals and alpha pairs in larger packs will howl less frequently than coyotes in smaller packs. Since the alpha pair performed most of the howling in the pack, it follows that pack size would not influence howling rates in resident coyote packs. We found that the howling rates of individual coyotes in the pack, as well as of the alpha pair, were independent of pack size.

Communication via vocalization is common among social carnivores. Little was known about the influence of social organization, social rank, and pack size on rates of long-range coyote vocalizations, primarily because of the secretive and nocturnal nature of coyotes, which makes observations of free-ranging animals difficult. Our observations of coyotes in Yellowstone National Park indicated that social organization, social rank, and season were important determinants of coyote vocalization rates. Our results parallel findings for other social carnivores, particularly wolves. Among coyotes, howling plays a role in territorial maintenance and pack spacing by advertising territorial boundaries and signalling the presence of alpha animals that will confront intruders and defend the territory. In these large packs, at times as large as 10 coyotes (Gese et al. 1996b, 1996a), the alpha pair performed most of the howling in the pack, while subordinate members were less likely to howl. Hence, pack size did not influence howling rates. The repertoire of vocalizations among large carnivores is vast and what these howling events communicate to other animals is still debatable. However, with continued direct observation of known individuals in free-ranging populations of social carnivores, answering these and many new questions will increase our understanding of animal communication.

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